

Telocytes: history, character and importance in medicine

An update on telocytes characters and importance

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Abstract

Telocytes (TCs), recently identified interstitial cells, have been frequently investigated in many researches. This review summarized, in brief, the morphological features, distribution, immunohistochemical, and genomic characteristics of TCs. This review identified in brief the difference between Telocytes and stem cells. The functions of TCs and their potential application in regenerative medicine have been reviewed. The genetic analysis of TCs and the functional relationship with other neighboring cells including stem cells were also briefly described. Many future researches are still needed to discover more about the telocytes and its utilization in improving the fate of regenerative medicine.

Keywords

Telocytes; History; Structure; Electron; Microscope; Function; Stem Cells; Fibroblasts

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Introduction

Telocytes (TCs) are considered recently discovered interstitial cells characterized by having very elongated, thin cellular prolongations called telopodes have alternating thin segments (podomers) with dilatations (podoms) [1]. When the TCs were initially recognized by Popescu et al. they were named “cells with telopodes” [2].

When the electron microscope (EM) was utilized, the special interstitial cell type was found to coincide with cells that were described by Cajal in the early 1970s. These cells were present in the gut muscle coat, later on, it was clear that they were not neurons, and were noted ‘interstitial cells of Cajal’ (ICC) [3].

Since their discovery in 2010, TCs were frequently studied. About 132 records have been found to describe “telocyte” from 2010 to 2015 and they have been cited in the Web of Science more than two thousand time [4]. On routine histological examination using light microscopy, TCs could not be discriminated from the surrounding fibroblast-like cells due to the similarity in appearance and proximity to these cells [5].

Telocytes are distinguished from the other interstitial cell types “e.g. fibroblasts, fibrocytes, fibroblast-like cells, mesenchymal cells”, because of their prolongations, based on the morphological characters through electron microscope [6].

Sites of TCs:

Telocytes were initially described in mouse trachea and were successfully isolated and cultured from mouse lung tissues [7]. Telocytes have been identified in the interstitial space of many organs e.g. skin [8], exocrine pancreas [9], pericardium [10], pleura [11] uterus and fallopian tube [12], prostate [13], heart [14], kidney [15], intestine [16] stomach [17], liver [18], lung and trachea [19] and many other organs [4] (Figure 1).

Electron microscopic character of Telocytes:

Transmission electron microscopy (TEM), scanning electron microscopy (SEM), electron tomography, focused ion beam-scanning electron microscopy (FIB-SEM) are currently used techniques to localize in different organs and tissues (Figure 2). TEM still represents the “golden standard” in the identification of TCs (Figure 3) [6, 20]. Telocytes might be spindle, pyriform or triangular in shape and they possess many elongated long and thin processes that range from 1 to 5 per cell. The cell body shape of TCs is depending on the number of telopodes emerging from it as follows: the pyriform cell body has only one telopode, the spindle cell body possesses two telopodes, the triangular cell body has three telopodes, while the stellate cells have over three telopodes. The nucleus of TCs occupies about 25% of the cell body. It is oval in shape with no apparent nucleolus, while the heterochromatin masses are seen on the inner nuclear envelope. The nucleus is enclosed by a small amount of cytoplasm with Golgi complex, mitochondria, rough and smooth endoplasmic reticulum and cytoskeletal elements [6].

Cretoi et al. observed that TCs present in the jejunum of rat in 2 sites; the sub-epithelial lamina propria and in-between the smooth muscle fibers in the muscularis mucosae. Telopodes of the telocytes display podomeres and podoms (dilatations containing mitochondria and endoplasmic reticulum). Telopodes have dichotomous branching and make a three-dimensional network close to immune cells, smooth muscle cells or nerve bundles [21].

Telocytes also have numerous cytoskeleton components like the intermediate filaments and caveolae on the cell membrane,

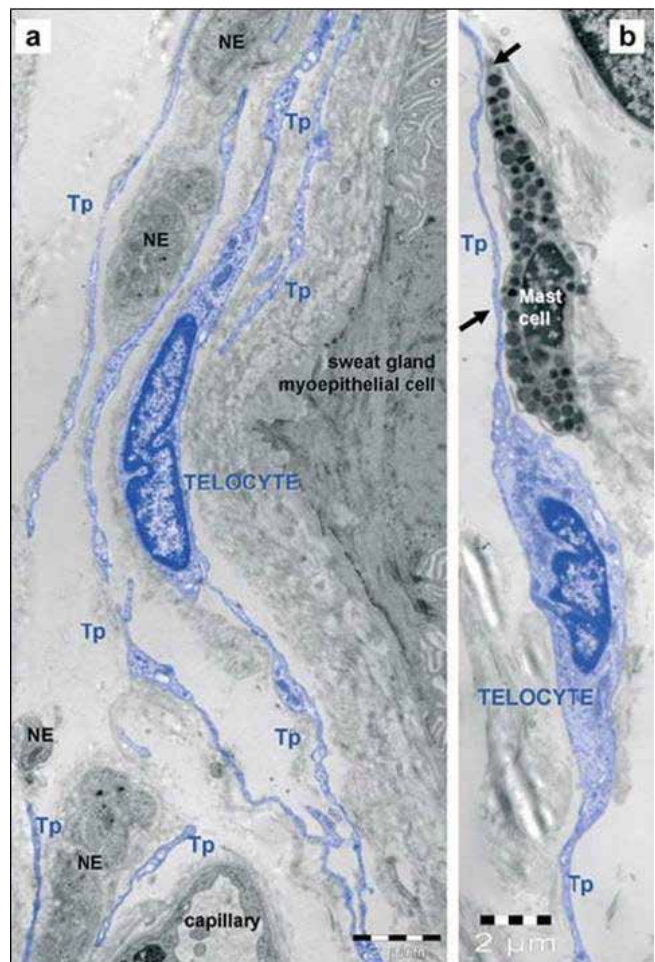


Figure 1. Telocyte layers in human skin appendages. Cited from Ceafalan et al. [5]

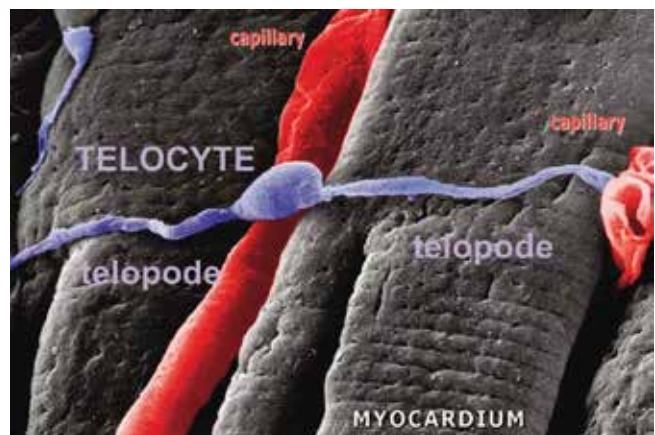


Figure 2. Representative scanning electron micrograph. Cited from Kostin and Popescu. [21]

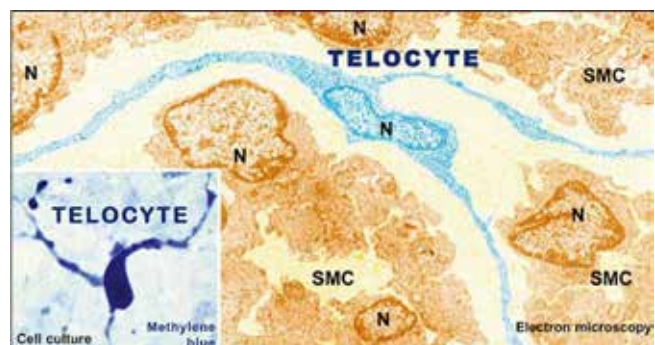


Figure 3. A telocyte show three processes with many beads along telopodes is colored in blue. The original magnification was 96800. Cited from Ciontea et al. [20]

while a basal lamina is lacking. The caveolae make up 2–3 % of the cell body and present ~ 0.5 caveolae/ μm of cell membrane length [6].

The presence of telopode is a distinguishable character of TCs to differentiate it from all interstitial cells like ICCs, fibroblasts, neuronal dendrites, and mesenchymal stem cells. Telopode is considered the longest process found in the tissue in comparison to some axons of certain neurons. Telocytes, via intercellular junctions “as a gap or adherens junctions”, may communicate with the surrounding TCs or other cell types to form “a 3D network, budding shed vesicles, and exosomes” [14].

Sequenced series of EM images are much better to visualize the ultrastructure of TCs because of their cellular prolongations (Figure 4) [22]. Intercellular signaling through secreting small molecules in the surrounding areas was observed to occur between TCs and the adjacent cells either in normal or pathological conditions [23]. Extracellular vesicles including essential macromolecules like RNAs or proteins were continuously shedded from the telocytes. Using TEM, three types of extracellular vesicles were recognized near the cardiac TCs based on their size. These vesicles are known as multivesicular cargos, exosomes, and ectosomes [23].

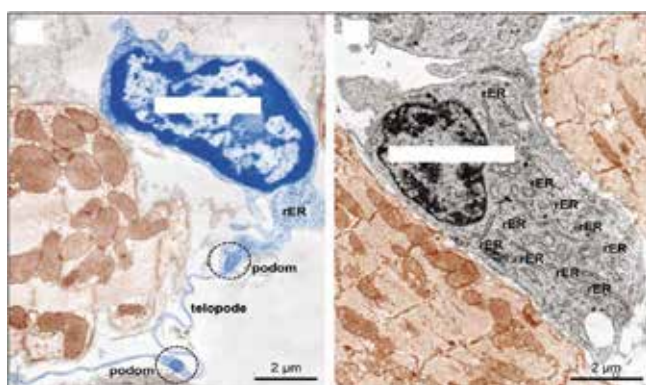


Figure 4. Three sequenced electron microscopy images of a telocyte. Cited from Bei et al. [22]

Immunohistochemical Identification of Telocytes:

Although there is no single specific immunostaining for identification of TCs available till now, double immunolabeling represents a current beneficial technique for TCs identification and assessment [24, 25]. Hematopoietic stem cell marker CD34/c-kit and CD34/vimentin, mesenchymal cell marker, are relevant immunomarkers for TCs [24].

Unfortunately, CD34 immunostaining does not provide clear identification of TCs as it does not stain all telocytes. However, it is the superior method, till now, to identify TCs when combined with vimentin or c-kit [26]. Tissue- and organ-specific immunomarker are now available for TCs [24]. Cardiac TCs were described to express “CD34, vimentin, myocardial stem cell markers sca-1 and c-kit, and embryonic stem cell-associated gene of Nanog” [30].

Telocytes could be immunohistochemically differentiated from many other interstitial cells as they are negative for fibroblasts-specific markers (CD90/Thy-1) and endothelial cells-specific markers (procollagen 1, CD31/PECAM-1). In addition, TCs are negative to α -SMA which is essentially expressed by vascular smooth muscle cells, myofibroblasts, pericytes and are negative to CD68, CD1a and CD62-P which are essentially expressed by macrophage [24, 26].

It was reported that TCs observed in skeletal muscle expressed platelet-derived growth factor receptor- β (PDGFR- β). These TCs control microvessel cell recruitment during angiogenesis [7, 27]. Thus, “double positive immunostaining with CD34/PDGFR- β is considered a suitable marker for the detection of TCs in the esophagus, corpus and antrum, gastric fundus, liver, and intestine” [26, 28, 29].

Splenic TCs were reported to have vimentin, CD34, Nanog, and sca-1 antigens but they do not have c-kit [30]. Podoplanin (D2-40) was considered as a marker of telocytes in the bladder” although it could not be a single reliable marker for these cells and should be combined with other markers as it is normally expressed by other cells like chondrocytes and osteocytes [31].

Genomics of TCs:

TCs are regarded as a special type of interstitial cells with developmental and functional characteristics that differ from both the mesenchymal stem cells and the fibroblasts as they express different genes from these cells.

Several up-regulated genes were recognized in telocytes like “transgelin (Tagln), matrix metalloproteinase 10 (Mmp10), retinol-binding protein 1 (RBP1), nidogen 1, connective tissue growth factor (CTGF), tissue inhibitor of metalloproteinase 3 (TIMP3), collagen type IV, alpha and matrix metalloproteinase 3 (Mmp3)”. All these genes recorded to have an essential role in tissue remodeling and repair [32].

The microRNA signatures have been studied in cardiac cells by Cismasiu et al. and they observed “the alteration in microRNA expression between telocytes and cardiomyocytes [33]. Telocytes keep the mesenchymal origin by considerably up-regulating miR-21, miR-22, miR-29, and miR-199a-5p and down-expressing miR-1, miR-133a, and miR-208a”. Proteomic analysis of human lung TCs was conducted by Zheng et al. in comparison with fibroblasts and they found that myosin-4, periplakin, and oxidoreductase activity linked proteins are up-regulated in TCs [34].

What are the differences between Telocytes and fibroblasts?

Based on the structure elicited using the EM as well as gene expression profile, TCs are clearly distinguished from the fibroblasts. More than 2000 genes were found to be up-regulated and > 4000 genes were down-regulated in telocytes in comparison to mesenchymal stem cells and fibroblasts”. When it comes to the function, TCs are concerned with the intercellular signaling, through connection with the nearby components or through the release of extracellular vesicles. On the other hand, fibroblasts function is mostly concerned with the formation of collagen and other matrix components [23].

Regarding the differences in shape between TCs and fibroblasts, in contrast to the shape of the TCs described above, the fibroblasts are spindle-shaped, possess a large amount of cytoplasm, a single oval nucleus with typically euchromatic chromatin and one or two nucleoli (Figure 5). The fibroblasts have prominent Golgi apparatus, the smooth endoplasmic reticulum (ER) nearly lacking, but rough ER is noticeable, present mostly in cell body but also in processes. Caveolae are hardly seen in the fibroblast and no junctions could be detected with other cells. The fibroblast usually shows 2 tapered -ends prolongations with several micrometers with neither podomers nor podoms [18].

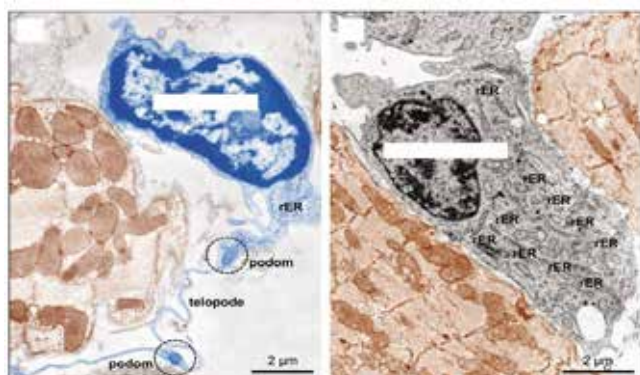


Figure 5. Digitally colored electron micrograph of rat ventricular myocardium. Reproduced with permission from Kostin et al. [21]

The relationship between telocytes and stem cells:

TCs were described, based on many studies, to be involved in tissue development, homeostasis, and occurrence of diseases [35]. Based on their situation, near stem cells or progenitor cells in many tissues like skeletal muscle, heart, choroid plexus, lung, skin, meninges, liver eye, TCs were proposed to be responsible for tissue renewal [29, 36].

The concept of the possible role of telocytes in tissue renewal after the damage was reported in many previous studies [37]. TCs also were described to show stem cell markers like c-kit, Sca-1, and Oct 4. Although expression of these stem cell markers was different in tissues, this proposes a crucial role of TCs in regeneration [24].

Establishment of a good microenvironment that helps survival, dissemination, and renewing potential of the injected stem cells is crucial for the success of both stem cells and the progenitor cells applications in regenerative medicine [38].

There is still a controversy between researchers regarding the mechanism of interaction between stem cells and telocytes. Among the hypotheses suggested to explain this relation was that of Zheng et al., who proposed direct cell to cell signaling and close cross talk as telocytes may afford antioxidant protective effect to stem cells [34]. In addition, TCs also expressed both in situ and in vitro vascular endothelial growth factor and PDGFR-b, explaining their potential effect in angiogenesis during tissue repair [7].

Caafalan et al. proposed that TCs have a role in the differentiation of mesenchymal SC [5]. On the other hand, Zhao et al. claimed that telocytes might be a subpopulation of mesenchymal stem cells because they have some markers of stromal niche cells [39]. Not only that, but telocytes were suggested to play a vital role in cell signaling, therefore adjusting the microenvironment in intact as well as diseased tissues [40].

Li et al. claimed that adding TCs to stem cell niches, in certain tissues, will help to create “a compound interstitial network with resident stem cells, nerve endings, blood vessels as well as other interstitial components which can participate in tissue renewal [37].

Importance of TCs:

Among the postulated roles of TCs, was “in juxta signaling” - or “paracrine signaling” [9]. It was evidenced that telocytes are able to create both homocellular and heterocellular junctions and can release extracellular vesicles [18, 21]. TCs could mechanically support the surrounding structures as they possess a three-dimensional structure. They can regulate the blood vessel closing in rat mesentery. Another proposed function of TCs

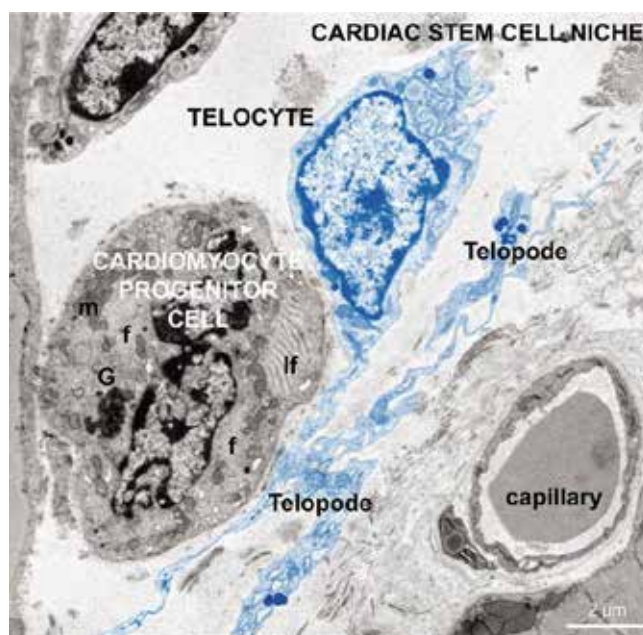


Figure 6. Electron microscopy micrographs from epicardial stem cell niche. Reproduced with permission from Gherghiceanu and Popescu. [14]

in the neuromuscular spindles was the regulation of muscular tone [42]. TCs might control and adjust the tissue remodeling activity performed by mesenchymal cells, neural stem cells and myocardial precursors [43].

Being closely related to the cardiomyocyte progenitors, cardiac stem cells, TCs were thought to be important for the proliferation and differentiation of myocardial precursors into new cardiac muscle fibers in both intact and injured heart as well as for new blood vessels formation (Figure 6) [44, 45]. TCs in the lung possess the latent participation in tissue homeostasis, stem cell niche modulation, reserving oxidative stress, and delaying cellular aging [34].

It was reported that smooth muscle fibers are electrically joined to ICC, thus TCs were proposed to be involved in neurotransmission as well as “spreading the slow waves generated by the ICC” [17]. TCs also were reported to be involved in supplying data required for the immune response [32]. In the reproductive system, telocytes are described to have estrogen and progesterone receptors and hence were involved in coordinating the contractility and proliferation of smooth muscle cells [41].

Decreased number of telocytes was evident in the fibrotic areas in experimental myocardial infarction [39]. Zhao et al. have reported that “intramyocardial transplantation of telocytes from the heart can reduce myocardial infarction and recover post-infarcted cardiac function through enhancing cardiac angiogenesis and reconstruction of the telocytes networking and reducing cardiac fibrosis” [46].

Tissue engineering and regenerative medicine community possess great expectations for TCs in the regenerative medicine. The TCs are possibly innovative target for therapeutic strategies as advanced molecular and cellular researches on TCs roles might give new tools for regenerative potential of damaged organ [40, 47].

Summary: Although telocytes were recently discovered, they have been investigated frequently to identify their morphological features, distribution, immunohistochemical and genomic characteristics, the difference in their structure compared to other cells like fibroblasts and stem cells. TCs perform many important functions like supporting the surrounding structures, controlling, and adjusting the tissue remodeling activity besides

other tissue-specific functions. Their functions and potential application in regenerative medicine have been also studied. The genetic study of telocytes on many organs and the functional connection with other adjacent cells as the stem cells were also described. Many future researches are still needed to discover more about the telocytes and its utilization in improving the fate of regenerative medicine.

Scientific Responsibility Statement

The authors declare that they are responsible for the article's scientific content including study design, data collection, analysis and interpretation, writing, some of the main line, or all of the preparation and scientific review of the contents and approval of the final version of the article.

Animal and human rights statement

All procedures performed in this study were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. No animal or human studies were carried out by the authors for this article.

Conflict of interest

None of the authors received any type of financial support that could be considered potential conflict of interest regarding the manuscript or its submission.

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